



# Metabolism and cold tolerance of overwintering adult mountain pine beetles (*Dendroctonus ponderosae*): Evidence of facultative diapause?

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## ABSTRACT

We sought evidence for a distinct diapause in adult overwintering mountain pine beetles (*Dendroctonus ponderosae* Hopkins) by measuring metabolic rate and supercooling ability of field collected beetles throughout the year. Metabolic rates measured at 0, 5, and 10 °C declined significantly from October through November, then rose slowly, reaching levels as high as those recorded in October by late May. From December to February metabolic rates were not correlated with minimum weekly phloem temperatures ( $R^2 = 0.0\%$ ,  $P = 0.592$ ), but were correlated with phloem temperatures as winter advanced to spring ( $R^2 = 44.8\%$ ,  $P = 0.010$ ), a pattern consistent with progression through the maintenance and termination phases of diapause. Supercooling points were also significantly lower in winter compared to fall and spring ( $F_{(8,143)} = 32.6$ ,  $P < 0.001$ ) and were closely correlated with metabolic rates ( $R^2 > 79\%$  for all three temperatures). Dry mass declined linearly with winter progression ( $F_{(8,150)} = 8.34$ ,  $P < 0.001$ ), explained by catabolism of metabolic reserves, with a concomitant accumulation of metabolic water ( $F_{(8,147)} = 35.24$ ,  $P < 0.001$ ). The strong mid-winter metabolic suppression correlated with improved supercooling ability, coupled with their lack of response to variation in environmental temperature, are evidence of possible diapause in adult overwintering mountain pine beetles.

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## 1. Introduction

The physiology of overwintering mountain pine beetles, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae), is not well understood. This species occupies a range that spans western North America from southwestern United States to the provinces of British Columbia and Alberta (Reid, 1962; Carroll et al., 2004). In the last century their range has, and continues to, increase in latitude and altitude into previously unsuitable habitat (Safranyik et al., 1975; Carroll et al., 2004). It is believed that overwinter survival is a key factor limiting their range. Thus, elevated annual winter temperature minima due to climate change are considered an important influence on their range expansion, as well as on increases in outbreak frequency and severity (Safranyik, 1978; Cole, 1981; Logan et al., 1995; Logan and Powell, 2001; Campbell et al., 2007; Aukema et al., 2008). Determining how mountain pine beetles overcome the physiologic challenges associated with extreme winter conditions is critical in forecasting future outbreaks and predicting their long term impact, especially during this period of warming temperatures. Diapause is an energetically efficient form of dormancy which reduces energy loss during periods of inactivity due to adverse conditions (Mansingh, 1971). Despite its

potential importance, evidence for the presence or absence of diapause, in the mountain pine beetle remains equivocal. Populations in the northern or subalpine portions of their range overwinter in cold climates which reduce energy demand in non-diapausing insects. However, populations exposed to milder winters in the temperate part of their range may experience increased energetic stress, leading to a decline in outbreak intensity and frequency in populations occupying these areas in the absence of diapause-related metabolic suppression or periodic feeding during permissive temperatures.

Insects, such as mountain pine beetles, that occupy regions with seasonal, environmental variation must cope with cyclic periods of ecological adversity. Energy conservation is an important factor, often essential, for survival and reproductive success (Pullin and Bale, 1989; Irwin and Lee, 2003) during extended periods of food deprivation. Dormancy permits insects to endure such events by reducing energetic demands during episodes of food scarcity and deleterious conditions, and also by providing insects with a method of phenological synchronization (Danks, 1987). The most prevalent forms of insect dormancy are quiescence and diapause (Mansingh, 1971). Quiescence is defined as dormancy resulting from a direct and immediate response to adverse environmental conditions, lacking a preparatory phase, and with immediate resumed development upon exposure to permissive conditions. Quiescence prevails in temperate regions where dormancy is required for brief, spontaneous adverse conditions (Mansingh, 1971; Danks, 1987; Košťál, 2006).

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Diapause is a hormone-regulated dormancy in preparation for anticipated adverse conditions that are cyclic in nature, characterized by arrested development and significant metabolic suppression. In the discussion that follows, we present the phases of diapause as described by Košťál (2006), but add the equivalent classification by Mansingh (1971) parenthetically for those familiar with that classification scheme. Diapause is divided into multiple phases: the induction phase, the preparation (preparatory) phase, maintenance (refractory) phase, the termination phase, and post-diapause quiescence (activated phase). The induction phase is the period of sensitivity to diapause inducing environmental signals, referred to as token stimuli, which may initiate the diapause response individually or in combination with multiple signals. The preparation phase is a period of direct development which precedes the initiation phase and permits biochemical adjustments and fortification of metabolic reserves to occur before the onset of adversity. Some species do not experience this phase. Initiation is the early phase of diapause, characterized by cessation of morphogenesis and endogenous suppression of metabolism (Danks, 1987). Following initiation, diapause enters a phase where it is maintained for a period of time until the conditions for termination are met. Throughout this maintenance (refractory) phase individuals remain in developmental arrest and metabolic rates continue to be suppressed, even in the presence of favorable environmental conditions (Mansingh, 1971; Košťál, 2006). The termination phase is controlled by a token stimulus or stimuli, similar to the induction phase, and is related to the potential for resumption of development and advancement into post diapause quiescence where development may resume in the presence of favorable conditions (Hodek, 1996; Košťál, 2006). Diapause in insects likely exists in a continuum of variation, where the duration of these phases and the sensitivity to environmental cues differ among species, populations and individuals making detection sometimes difficult.

Studies focused on mountain pine beetle development have been unable to provide evidence for diapause in this species. Safranyik and Whitney (1985) showed that mountain pine beetle larvae undergo developmental arrest when incubated at low temperatures, but they soon resumed development after being exposed to favorable conditions. However, these beetles were incubated at low temperatures for 113 days, a period likely to cause them to progress through the maintenance phase to the post-diapause quiescence phase, resulting in little delay before resuming development. It has also been shown that diapause is not essential for completion of development (Reid, 1962; Safranyik and Whitney, 1985), providing evidence against obligate diapause, but not eliminating the possibility of facultative diapause. Additionally, Bentz et al. (1991) showed that life stage synchronization in mountain pine beetles was accomplished by direct temperature control, where different minimum temperature thresholds for development were associated with different life stages. A specific range of environmental temperatures suspended or retarded development for later stage larvae, while the development rate of earlier stages is maintained, accelerating their relative progress. These studies demonstrated that diapause was not induced or detected under the experimental conditions created by the researchers and that it was not necessary for development, but do not provide sufficient evidence against facultative diapause in naturally reared mountain pine beetles. The spruce beetle (*Dendroctonus rufipennis* Kirby), which is a closely related *D. ponderosae* congener, similarly has flexible voltinism and development which are controlled directly by temperature rather than by diapause (Hansen et al., 2001). However, this species is capable of facultative larval (prepupal) diapause, induced by incubation at cold temperatures (Dyer and Hall, 1977) or through thermoperiod variation (Dyer, 1970). Thermoperiod is the daily temperature cycle which varies seasonally and may be used by organisms either as a proxy

for photoperiod or to enhance sensitivity to it. This stimulus may be critically important for species who occupy microhabitats relatively isolated from sunlight, e.g. bark beetles. Thermoperiod has not been tested as a token stimulus in mountain pine beetles, yet it is capable of inducing diapause in a closely related species, which, at least in parts of its range, experience similar environmental conditions. Seasonal variation in host tree chemistry is another possible and potentially important token stimulus which has not been evaluated in mountain pine beetles. The limited experimental testing of possible token stimuli in previous studies requires further investigation to eliminate the possibility of facultative diapause in mountain pine beetles.

Consideration must be made for the selective pressure on overwintering insects for the conservation of energy reserves. Irwin and Lee (2003) demonstrated that a slight increase in metabolic rate due to higher environmental temperatures strongly affects survival and reproductive success in the goldenrod gall fly (*Eurosta solidaginis* Fitch). Overwintering larvae exposed to lower temperatures experienced lower metabolic rates thereby reducing the consumption of energetic reserves resulting in an increase in survival and fecundity. The spruce bark beetle, *Ips typographus*, has also shown increased mortality when overwintering at 5 °C compared to -5, -10, or -15 °C (Košťál et al., 2011). Similarly, mountain pine beetles experience reduced fecundity when exposed to energetic stress. Elkin and Reid (2005) showed a significant decrease in egg size when females were starved and forced to expend energy on non-reproductive maintenance. Body mass prior to reproduction in starved individuals was less than their non-starved counterparts, yet the two treatment groups did not differ significantly in post-reproductive mass, suggesting the difference in mass was due to egg production and pre-reproductive energetic stores, and starved individuals sacrificed reproductive output to maintain somatic condition. This association between the depletion of metabolic reserves and fecundity reveals the tight energetic constraints experienced by overwintering insects, and demonstrates the advantages of metabolic suppression provided by diapause.

Mountain pine beetles are unable to tolerate the formation of ice within their tissues and therefore must avoid freezing, yet display low mortality from exposure to temperatures above their supercooling point (Bentz and Mullins, 1999), a characteristic of freeze avoiders (Bale, 1993). Supercooling point depression is the reduction of the temperature of ice crystallization ( $T_C$ ) in the body fluid, typically accomplished in insects by voiding their gut of ice-nucleating agents and undergoing biochemical adjustments (Lee, 1991). As autumn advances, mountain pine beetles accumulate carbohydrates, primarily glycerol (Bentz and Mullins, 1999), in their hemolymph and bodies, which act as a cryoprotectant in this species and have been shown to reduce desiccation in other species (Sømme, 1964; Lee, 1991; Ring and Danks, 1994). Although insects may actively depress their  $T_C$  as a survival strategy, carbohydrate accumulation and supercooling point depression have also been correlated with diapause (Denlinger, 1991; Milonas and Savopoulou-Soultani, 1999), diapause-related metabolic suppression in insects (Pullin et al., 1991; Pullin 1992), and has been shown to occur in the absence of drought or temperature-related stress (Pullin and Wolda, 1993). Pullin (1996) posited that carbohydrate accumulation may be a byproduct of metabolic suppression in primitive insects occupying warm climates, and an exaptation for desiccation resistance and cold tolerance before insects radiated toward more inhospitable regions. Diapausing insects that colonized environments which exposed them to arid or sub-freezing conditions would have had a strong selection force to conserve and further improve this trait. In the context of overwintering, it is reasonable to predict that many insects capable of extensive cold hardening through the accumulation of cryoprotectants (such as mountain pine beetles) do so as a direct result of endogenous metabolic suppression.

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